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Environmental control of growth and flowering of *Rubus idaeus* L. cv. Glen Ample

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ABSTRACT

Environmental control of the annual growth cycle of 'Glen Ample' raspberry has been studied in order to facilitate crop manipulation for out-of-season production. Plants propagated from root buds were raised in long days (LD) at 21 °C and then exposed to different temperature and daylength conditions at varying ages. Shoot growth was monitored by weekly measurements and floral initiation by regular sampling and examination of axillary bud #5. Under natural summer daylight conditions at 60°N shoot growth was nearly doubled at 21 °C compared with 15 °C, while at 9 °C one half of the plants ceased growing and formed flower buds at midsummer. Developing shoots have a juvenile phase and could not be induced to flower before the 15-leaf stage. No significant reduction in induction requirements was found in larger plants. Plants exposed to natural light conditions from 10th August, had an immediate growth suppression at 9 and 12 °C with complete cessation after 4 weeks (by September 7). This coincided with the first appearance of floral primordia. At 15 °C both growth cessation and floral initiation occurred 2 weeks later (by September 21), while at 18 °C continuous growth with no floral initiation was maintained until early November when the photoperiod had fallen below 9 h. The critical photoperiod for growth cessation and floral initiation at 15 °C was 15 h. Plants exposed to 10-h photoperiods at 9 °C for 2–4 weeks had a transient growth suppression followed by resumed growth under subsequent high temperature and LD conditions, while exposure for 5 or 6 weeks resulted in complete growth cessation and dormancy induction. The critical induction period for floral initiation was 3 weeks although no transitional changes were visible in the bud before week 4. When exposed to inductive conditions for marginal periods of 3 or 4 weeks, an increasing proportion of the plants (20% and 67%, respectively), behaved as primocane flowering cultivars with recurrent growth and terminal flowering. It is concluded that growth cessation and floral initiation in raspberry are jointly controlled by low temperature and short day conditions and coincide in time as parallel outputs from the same internal induction mechanism.

1. Introduction

The red raspberry (*Rubus idaeus* L.) is a temperate species that bears short-lived woody shoots on a long-lived perennial root system. In the common biennial fruiting cultivars the shoots (canes) have a 2-year life cycle during which each shoot passes through a sequence of seasonal phases involving vegetative growth, flower initiation and development as well as induction and breaking of bud dormancy. In the so-called primocane fruiting cultivars, on the other hand, the cycle of vegetative growth, flowering and fruiting is completed in one single growing season. These aspects have recently been reviewed by Carew et al. (2000).

The morphology and seasonal development of the biennial raspberry were studied and described in detail by Hudson (1959) and, in an associated series of papers, aspects of the underlying environmental control of the various stages were investigated by Williams (1959a,b,c, 1960). These studies were confined to the cultivars Malling Promise and, to a lesser extent, Lloyd George, which are both largely replaced by new cultivars today.

Shoot growth of the raspberry plant requires the combination of high temperature and long photoperiods. Thus, at high temperature (21 °C) 'Malling Promise' plants grew continuously in both 9- and 14-h photoperiods, at 10 °C they ceased growing in both daylengths, while at 15.5 °C growth cessation took place in short day (SD) only (Williams, 1959b). Nestby (1986) demonstrated that

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even under natural continuous light conditions at high latitudes, raspberry plants ceased growing and became dormant at low summer temperatures of about 10 °C. Under natural environmental conditions initiation of floral primordia occurs in the autumn. Waldo (1933) reported that in Oregon, USA, the cultivars Cuthbert, Marlboro and Lloyd George had all differentiated flower buds by November. Similarly, Mathers (1952), Wood and Robertson (1957) and Robertson (1957) in Scotland found that while 'Malling Promise', 'Malling Landmark' and 'Lloyd George' were entirely vegetative in July, they had all initiated floral primordia by middle of September. These results were confirmed by Williams (1959c) who found that in 'Malling Promise' flower initiation of terminal buds was first seen in the second week of September after the elongation of the shoot had ceased. At nearly the same time flower initiation took place also in axillary buds in the region 5–10 nodes below the apex. Thereafter initiation took place in buds progressively lower down the shoot. By early December floral primordia were observed in all axillary buds except the lowest 10–12, and by the end of January in all buds above soil level (Williams, 1959c). In controlled environment 'Malling Promise' initiated flower buds at 10 °C in both 9- and 16-h photoperiods after 3 and 4 weeks, respectively. At 13 °C initiation occurred after 6 weeks and in 9-h photoperiod only, while at 15.5 °C no initiation took place regardless of the photoperiodic conditions (Williams, 1960). It was also demonstrated that the shoots have a juvenile phase during which they are not able to respond to environmental signals. Plants with 20 nodes initiated terminal flower buds after 2 weeks of inductive treatment at 10 °C and SD, and with three or more weeks of induction they all developed both terminal and lateral flower buds. Only some plants with 15 nodes initiated flower buds after 5 or more weeks of induction, while plants with five nodes were unable to undergo floral induction (Williams, 1960). However, plants with 30 nodes initiated both terminal and lateral flower buds after only 1 week of inductive treatment, suggesting that the conditions might have been marginally inductive during the preceding raising period and thus, could have confounded the effect of plant age and size.

Raspberry also has a clear pattern of seasonal dormancy in temperate climates. Under natural conditions at northern latitudes the deepest state of dormancy occurs in October and November (Williams, 1959b; Måge, 1975), the condition being induced by the combination of low temperature and SD (Williams, 1959b). While growth cessation in 'Malling Promise' took place after only 2 weeks at 10 °C and 9-h SD, the establishment of dormancy required more than 10 weeks at the same conditions. In fully dormant plants which had received 16 weeks of such low temperature and SD conditions, 6–8 weeks of chilling at 3–4 °C were required for breaking of dormancy and resumption of growth (Williams, 1959b).

Due to introduction of new cultivars and new and diversified production methods, red raspberry production for fresh consumption has expanded significantly in the UK and elsewhere in Western Europe during the resent years (Raffle, 2004). An important development has been the use of plastic tunnels for out-of-season production and protection of the crop. The cultivar Glen Ample released in 1996 (Stephens, 2006), has become very popular for this use, and is presently the most widely grown raspberry cultivar in the UK (Stephens, 2006) as well as in Norway (Heiberg et al., 2002). These new developments have greatly extended the harvesting and marketing season and improved the profitability of the crop (Raffle, 2004). However, change to protected cultivation with possibilities for manipulation of the annual growth cycle has also high-lighted the need for further understanding of the environmental responses of the crop (Brennan et al., 1998; Carew et al., 2000), especially those of the new and most widely grown cultivars. Therefore, we have studied the effects of temperature and photoperiod under controlled environment conditions on the control of the various developmental phases of the red raspberry cv. Glen Ample.

2. Materials and methods

2.1. Plant material and cultivation

The experiments were performed in the Ås phytotron (60°N, 11°E) in daylight compartments combined with adjacent growth rooms for photoperiodic manipulation. Red raspberry plants (*Rubus idaeus* L.) cv. Glen Ample were established from root buds and raised at 21 °C in continuous light (24-h photoperiod) in 3 l plastic pots filled with coarse-textured sphagnum peat with a pH of 5.8. In Experiment I which lasted for more than 5 months, the plants were transplanted into 5 l pots, using the same sphagnum peat compost. During the establishment period the plants were fertilized twice weekly, at later stages every second day, with a complete fertilizer solution (conductivity 1.8 dS m^{-1}), and otherwise watered with tap water as required.

Throughout the raising and experimental periods the plants were grown in daylight phytotron compartments. In Experiment I and IV the plants were grown in natural photoperiods throughout the experimental period. In the other experiments the plants were grown in natural daylight from 08.00 h to 18.00 h and were then moved into adjacent growth rooms with darkness, or with low-intensity light (6 μmol quanta m^{-2} s^{-1} given by 75 W incandescent lamps) for daylength manipulation. Whenever the quantum flux in the daylight compartments fell below 150 μmol quanta m^{-2} s^{-1} on cloudy days, an additional 125 μmol quanta were automatically added using Philips HPT-I 400 W lamps. Temperatures in the phytotron were controlled to ±1 °C, and a water vapour pressure deficit of 530 Pa was maintained at all temperatures.

2.2. Experimental design and data observations

The experiments were fully factorial, of the split-plot design, with temperatures as main plots and photoperiods and, in some experiments, plant size or duration of treatments, as sub-plots. All experiments were replicated with three randomized blocks, each comprising 4 or 5 plants on a separate trolley (i.e. a total of 12 or 15 plants per treatment). Growth was monitored by weekly measurements of plant height and counting of leaf (node) numbers. Flower initiation was assessed by weekly collection and examination of axillary buds. Routinely, bud number 5 from the apex of each plant was slit off by a shallow longitudinal slit and stored on 70% ethanol until dissected and examined under a stereo microscope. This sampling technique did not affect the continued growth of the shoot and, since one to three new nodes were initiated weekly, depending on the temperature conditions, a new bud in position #5 was available each week. Flower initiation and differentiation were scored according to the stages shown in Fig. 1. Quantitative experimental data were subjected to analysis of variance (ANOVA) by standard procedures using a MiniTab® Statistical Software program package (Release 14, Minitab Inc., State College, PA, USA).

3. Results

3.1. Effects of temperature on shoot growth under natural daylength conditions (Experiment 1)

Plants with 10 leaves were exposed to natural light conditions and temperatures of 21, 15 and 9 °C from 4th May to 5th October